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14. ABSTRACT

This project capitalized on and extended data, methodologies, and partnerships formed under the ONR funded Effect of Sound in the Marine Environment (ESME). The work comprised two years of collaborative effort focusing on sophistication and refinement of the baseline auditory model developed previously by these team members under ESME and employed the same model architecture and organizational structure that proved successful in the ESME project. The impact modeling effort developed a modular approach paralleling that of the ESME projects in order to permit compatibility with the on-going ESME effort as it develops.

The specific objective of this project was to develop biophysically based models of the acoustic power flow from the water, through the tissues of the head and middle ear, into the cochlea, and ultimately to the sensory receptor cells (hair cells). These models allow us to estimate audiograms for multiple odontocete species from anatomical and mechanical measurements and to predict the excitation pattern within individual cochlea for a range of acoustic inputs as well as modeling stresses and strains on key cochlear tissues from over-stimulation.

15. SUBJECT TERMS

Anatomical dimensions of the head, middle ear, and cochlea, anatomical and mechanical measurements, Marine Environment , Marine Mammals, Beaked Whales and micro CT scanning

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Beaked Whale Hearing and Noise Impact Models**

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LONG-TERM GOALS

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At present, there are broad scientific and public concerns about potential impacts of human sound sources in the oceans. It is imperative for conservation purposes that we find some means of assessing as accurately as possible how marine mammals may be affected by anthropogenic noise in the oceans, but to achieve the necessary level of detailed insight known about hearing in land mammals would require acute experimentation on whales that is impossible for practical, regulatory, and ethical considerations. Therefore, we must invent alternative methods for obtaining reliable

underwater hearing and impact estimates. To accomplish this requires developing robust, marine-explicit auditory models.

The overall goal of this project is to improve our understanding of how acoustic power is coupled to the inner ear of cetaceans in order to better predict the normal hearing capabilities of these species as well as to better predict the impact of man-made sounds.

OBJECTIVES

This project capitalized on and extended data, methodologies, and partnerships formed under the ONR funded Effect of Sound in the Marine Environment (ESME). The work comprised two years of collaborative effort focusing on sophistication and refinement of the baseline auditory model developed previously by these team members under ESME and employed the same model architecture and organizational structure that proved successful in the ESME project. The impact modeling effort developed a modular approach paralleling that of the ESME projects in order to permit compatibility with the on-going ESME effort as it develops.

The specific objective of this project was to develop biophysically based models of the acoustic power flow from the water, through the tissues of the head and middle ear, into the cochlea, and ultimately to the sensory receptor cells (hair cells). These models allow us to estimate audiograms for multiple odontocete species from anatomical and mechanical measurements and to predict the excitation pattern within individual cochlea for a range of acoustic inputs as well as modeling stresses and strains on key cochlear tissues from over-stimulation.

SCIENTIFIC AND TECHNICAL APPROACH

To achieve this objective, the project had three defined aims::

- 1) Create computer models of the interaction of sound with the cetacean head.
- 2) Create computer models of acoustic power flow through the cetacean middle ear.
- 3) Create computer models of cetacean cochlear physiology.

Anatomical dimensions of the head, middle ear, and cochlear were determined using a combination of conventional and micro CT scanning. Material properties were determined by direct measurement of middle-ear and basilar-membrane stiffness. Stiffness was measured using piezoelectric force probes.

Head acoustic FEM models derived from scan voxel data for bone, blubber, and acoustic fats simulated beam patterns for transmission of acoustic sources placed at the ears.

An integrated middle-ear-cochlea model was created by representing the middle ear and the cochlea as coupled mechanical and hydromechanical systems. A one-dimensional cochlear model was used with acoustic parameters derived from

anatomical and stiffness measurements. Point-stiffness measurements were converted to volume compliance by treating the basilar membrane as a thin plate.

The maximum cochlear response from the integrated model was measured for multiple frequencies and an audiogram computed. The model was verified by comparing predicted audiograms to experimentally measured audiograms in control species.

The effort involved three integrated teams:

1) **An Anatomical Analyses Team** (WHOI) led by Darlene Ketten, to characterize head, middle, and inner ear structures of targeted odontocete species.

Aim: To develop a comparative CT and histologic data base of heads and ears for three major dolphin and whale groups: delphinids, phocoenids, and ziphiids.

2) **A Physiological Modeling Team** (BU) led by David Mountain will implement auditory response models using the anatomical data and develop species-specific TTS models.

Aim: To develop species specific auditory response models and acoustic impact simulation data for Ziphiid heads and ears

3) **A Visualization Team** (NRL) led by Roger Hillson will develop data visualization tools for use in analyzing the anatomical and simulation data generated by the WHOI and BU teams.

Aim: To create three-dimensional interactive simulations of sound propagation and impacts from impulse vs. continuous sound sources.

WORK COMPLETED

WHOI and BU teams worked jointly to identify anatomical features that have the best predictive value for acoustic responses; e.g., range and sensitivity, for 37 ears from two control species (*T. truncatus*, bottlenosed dolphins, and *P. phocoena*, harbour porpoise) and for 10 ears of two focal genera (*Ziphius cavirostris* and *Mesoplodon spp.*, beaked whales). In addition, parallel CT and/or histologic measurements of inner ear anatomy were also obtained from 5 species of land mammals and 5 species of baleen whales. Species-specific databases were developed for heads, middle ears and inner ears to facilitate export to ESME modules and web-based distribution as well as additions and revisions of prior, limited data on cetaceans as more individual and species hearing data become available.

Our models predicted that there should be a correlation between middle-ear stiffness and audiogram low-frequency characteristics. To test this hypothesis, we obtained middle-ear stiffness and audiogram low-frequency cutoff data for a number of terrestrial mammalian species from the literature. An analysis of this data demonstrated that there is a strong correlation between these two variables.

We completed middle-ear stiffness measurements in two odontocete species: harbor porpoise and bottlenose dolphin. Odontocete stiffness vs. low-frequency-cutoff data fell very close to the regression line for the terrestrial species which supports the hypothesis that the cetacean middle ear is functionally similar to the terrestrial middle ear.

Experiments on cetacean basilar membrane stiffness showed the basilar membrane stiffness gradient in cetaceans to be similar to that for some terrestrial mammals. The stiffness data were incorporated into an integrated model and produced a predicted audiogram that was very close to the experimentally measured audiogram for each species.

These results support our contention that acoustic power-flow models based on measurements performed on ears harvested from stranded cetaceans can be used to predict hearing ability in species for which audiograms are not available.

SUMMARY RESULTS

Accomplishments during the two funded years can be divided primarily into the following topics. Details of the accomplishments are listed in the articles cited for each which are published or in press (listed in bold):

- Completion of scans and histology for two control species (**Ketten et al. 2003; Ketten 2004; Norman et al 2005**)
- Completion of scans and histology for two beaked whale species
- Identification of spiral geometry correlates for high and low frequency ears (**Chadwick et al 2006**)
- Biochemical of fatty tissues associated with the lower jaw and ear regions were completed for one control and two beaked whale species (**Koopman et al 2006**)
- Sound speed measures were completed for one control species (**Prasad, 2003**)
- Middle ear stiffness measures in two control and one beaked whale species (**Mountain et al 2003; Miller et al 2006**)
- Inner ear stiffness measures in two control species
- Comparisons of fresh, fixed and frozen tissues from two control species to determine fidelity of measures across and conditions
- Completion of fly-through visualizations for 1 control species and CT data reduction algorithms developed for whole animal visualizations.

Anatomical Analyses

Data obtained by the WHOI group (Ketten Lab) were directed at developing appropriate protocols to provide consistent interspecies data sets and obtaining, using these protocols, complete head and inner ear anatomical descriptors that could be used for finite element modeling transmission characteristics for underwater signals. Complete data sets were obtained for both whole heads and ears of 10 harbour porpoises, 8 bottlenosed dolphins, and 10 beaked whales from ultra-high resolution CT and MRI images as well light and electron microscopic measurements. Additional ultra-high resolution images were obtained

In addition to these cetaceans, measurements of the inner ears of chinchillas, cats, bats, and mice were also measured in order to provide comparative data of the inner ear scalae, basilar membrane, and organ of Corti elements in common laboratory animals. Lastly, inner ears of elephants, blue whales, humpbacks, gray whales, minke whales and right whales were also imaged and the scans measured to determine whether the same suite of measures were feasible for baleen whales as well.

Fat Structure and Physical Properties

Beaked whale specimens in this project were also analyzed by Dr. Heather Koopman during her tenure as a postdoctoral fellow at WHOI to determine whether there are significant variations in the biochemical and structural features of jaw fats in beaked whales vs other odontocetes.

Sound speed measurements were obtained via Time of Flight techniques for excised tissues of harbour porpoises in a system designed by Dr. David Brown of U Mass at Dartmouth, Bioengineering Dept., and the data were published in the form of a MS thesis for Mr. Kunil Prashad. This project comprised the system development and measurement of sound speed in animal tissues. Two apparatus designed in this project can measure the speed of sound in solids and liquids within an accuracy of 2%.

Physiological Modeling

The BU team (Mountain laboratory) was successful in obtaining direct stiffness measures from all of the above species and demonstrated the utility of measurement from fresh, formalin fixed, and previously frozen material, which means there is a substantially enhanced potential data base for analysis of inner ears. The BU team adapted existing procedure and hardware for exposure of the basilar membrane in the exceptionally large and dense odontocete periotics and for direct displacement and stiffness measures of both the middle and inner ear components in odontocetes comparable to those previously obtained in land mammals. A piezoelectric actuator produces a sinusoidal displacement of the stapes. The force sensor measures the stapes force and stiffness is computed by taking the ratio of force to stiffness.

Visualization Team

Prototypical visualizations of dolphin heads were successfully produced by NRL from CT data provided by the WHOI team. More sophisticated, interactive visualizations will be developed through joint BU and NRL work on exported WHOI scan data and FEM derived modules for both normal and stressed auditory systems.

GENERAL RESULTS

Anatomical Functional Analyses

In order to improve our understanding of high vs. low frequency adaptations in mammalian ears the inner ear data from both odontocetes and mysticetes were employed in a, collaborative effort between the Ketten laboratory and the NIH/NIDCD laboratory of Dr. Richard Chadwick to investigate anatomical correlates of low frequency hearing (LF) focusing on to how inner ear spiral topology relates to LF sensitivities (Figs. 1, 2, Table 1).



Figure 1a. 3D reconstruction of a Pygmy Sperm Whale (*Kogia breviceps*) right ear bone obtained from high resolution CT scans of the head. The periotic is rendered transparent to show the actual position of the cochlear spiral and auditory nerve (VIIIth) in the periotic (top of image). The ear is shown in its normal anatomical position from a medial view.

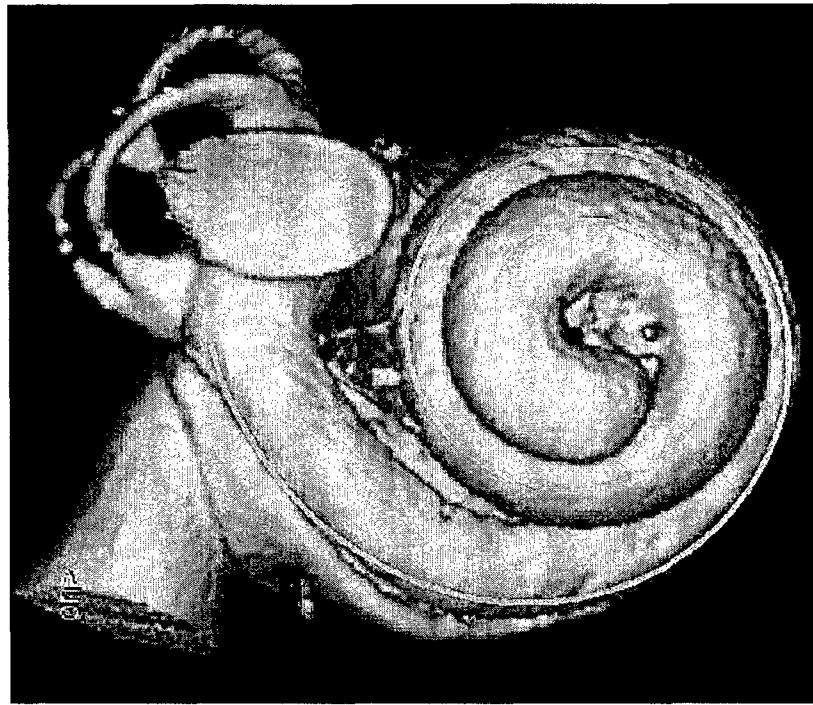


Figure 1b. Orthogonal projection of a Pygmy Sperm Whale (*Kogia breviceps*) right ear from in 3D reconstructions of CT scans. The superimposed yellow line represents the basilar membrane midline from which radii are measured. (Chadwick et al 2006)

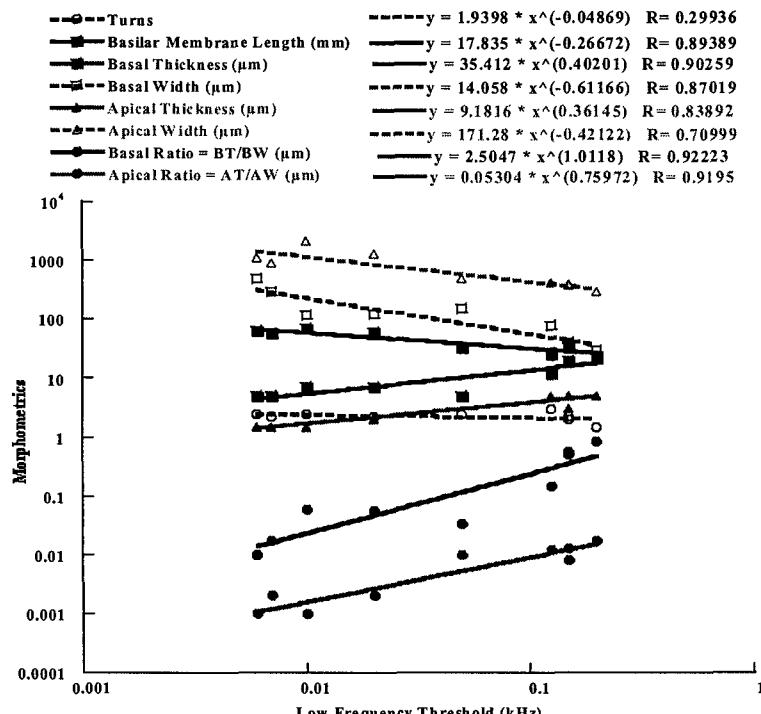


Figure 2. Cochlear morphometrics measured from CT scans and histology plotted in relation to low frequency limits of hearing for seven species of

cetaceans show basal and apical ratio are the best morphometric correlates of LF hearing (Ketten et al. 2006).

The principal conclusion is that the increase radii of lower frequency ears results in a "Whispering Gallery" phenomenon in which acoustic energy concentrates progressively along the peripheral walls, with incremental decrements in the nodal positions, resulting in a disproportionately high propagation of energy at lower frequencies at the apex. Thus the ratio of cochlear radii is a reliable metric for LF hearing abilities.

Table1
Radii ratios and low-frequency threshold

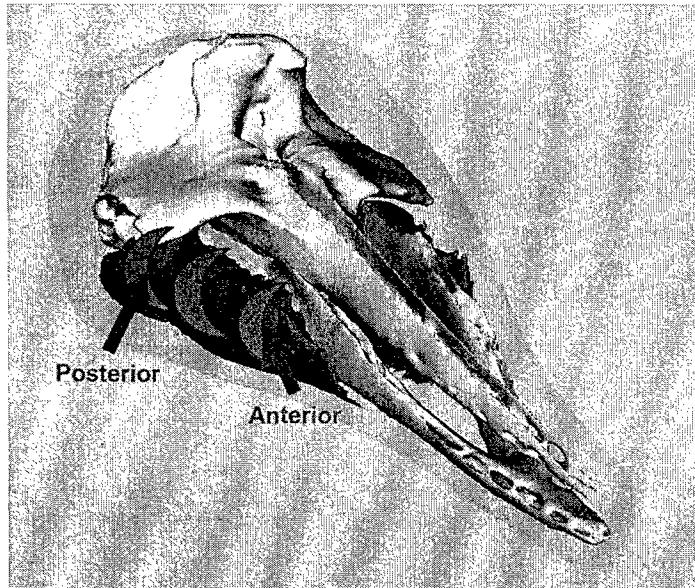
Species	blue whale	right whale	humpback whale	bottlenose dolphin	harbor porpoise
Rmax/Rmin	10.7	9.1	8.1	4.4	3.5
LF Hz	12	15	18	150	180
Species	african elephant	asian elephant	cow	guinea pig	man
Rmax/Rmin	9	8.7a	7.5	7.4	7
LF Hz	6	7	20	40	50
					400

Table 1. Cochlear radii ratios measured from CT scans and histology demonstrate a common trend of ratios being inversely related to LF hearing limits in both land and aquatic (Chadwick et al. 2006)

The fat studies showed consistent patterns in both the organization of lipids and in the related sound speed variations throughout the fat bundles. There is a repeatable and consistent variation by species in the percentage distributions of lipids. More surprising, however was the finding that there is a substantial, regimented topological regularity in the distribution of lipid types that creates an inner core which is present in both neonates and adults. There are variations in the absolute size according to age but proportionalities are relatively consistent suggesting that the basic pattern of these fats is set primarily ontogenetically.

The primary findings of the measures of sound speeds in excised fats from the jaw and melon were that all displayed a sound speed slightly below that of sea water (1386 to 1405 m/s at 25 degrees C) at an equivalent temperature (Fig. 3). There was also a consistent, linear decrease in the speed of sound with increasing temperature;

i.e., in direct contrast to the trend in water, and the speed is slowest in the highest fat content regions, all of which suggests that sound speed is not a result of well integrated tissues but rather that the lipids *per se* dominate the acoustic properties and propagation paths of both the jaw fats and the melon. The measurements support the theory that the acoustic fats have the potential to guide sound waves toward the cochlea. We also postulate that the skull has a role in providing directional hearing by baffling effects that may aid directional hearing. It is possible that the skull and ears can act as a two point baffled array.



Sample	Speed of sound in m/s at 25 C.
A1	1405
A2	1410
M1	1386
M2	1386
P1	1386
P2	1386

Figure 3a. Sound speeds measured at two samples in the anterior, middle, and posterior regions of mandibular fats in fresh post mortem odontocetes specimens. (see publications, Koopman et al 2006; Prashad 2003)

Head acoustic FEM models (Fig. 3b) were created using brick elements derived from scan voxels. Different material properties are assigned to bone, blubber, and acoustic fats. The head was simulated as though immersed in an infinite ocean. Point acoustic sources were placed at the ears and acoustic beam patterns measured

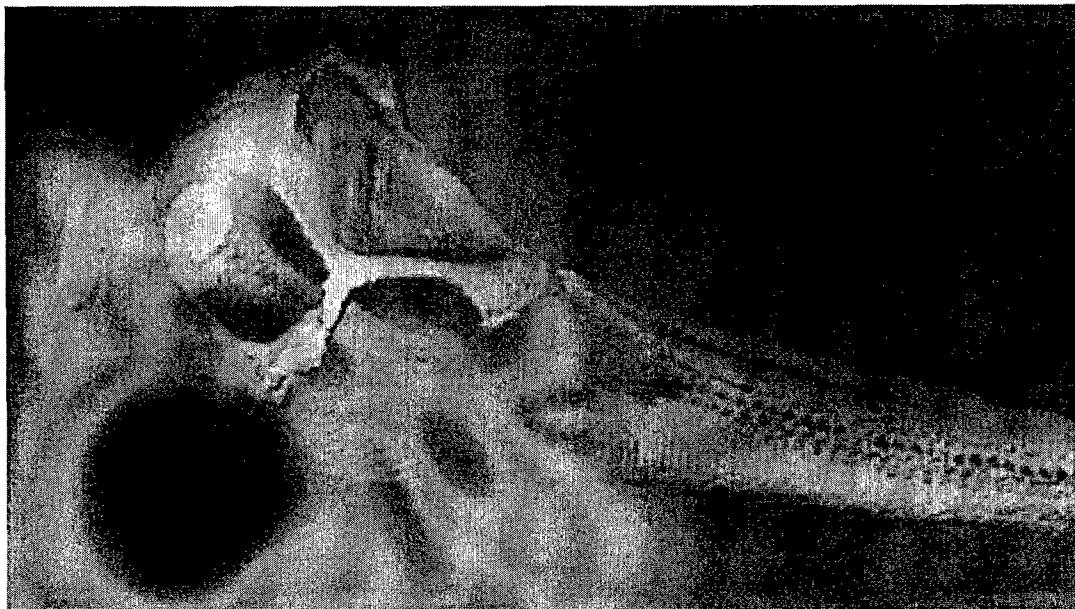


Figure 3b. FEM model of bottlenose dolphin acoustic beam pattern

Middle Ear Mechanics

In terrestrial mammals, the middle ear couples sound from the air to the cochlear fluids. The middle-ear transfer function (ratio of cochlear pressure to pressure in the ear canal) is believed to be a major factor in shaping the low-frequency portion of the audiogram. Since the role of the middle ear in cetacean hearing is a matter of considerable debate, we have been making a systematic series of measurements on odontocete middle ears and comparing our results to results from other species.

The low-frequency cutoff of the audiogram is a power function of middle-ear acoustic stiffness in terrestrial mammals. Odontocetes follow the general mammalian trend for high frequency species shows that the middle-ear acoustic stiffness for bottlenose dolphin and for harbor porpoise is close to the regression line for terrestrial mammals. This suggests that the cetacean middle ear functions in a manner similar to that of other mammals

Middle-ear Stiffness Measurements

Our biophysical models predict that there should be a strong correlation between middle ear stiffness and low frequency hearing cutoff as well as a correlation between basilar membrane volume compliance and the cochlear frequency-place map. These predictions are supported by extensive measurements in terrestrial mammals. Since the function of the tympanic membrane (tympanic ligament) in cetaceans has not been firmly established, we have developed a method for measuring middle-ear stiffness in cetaceans by exposing the stapes footplate and measuring stiffness from the cochlear side. The apparatus for making these measurements is shown in Figure 4.

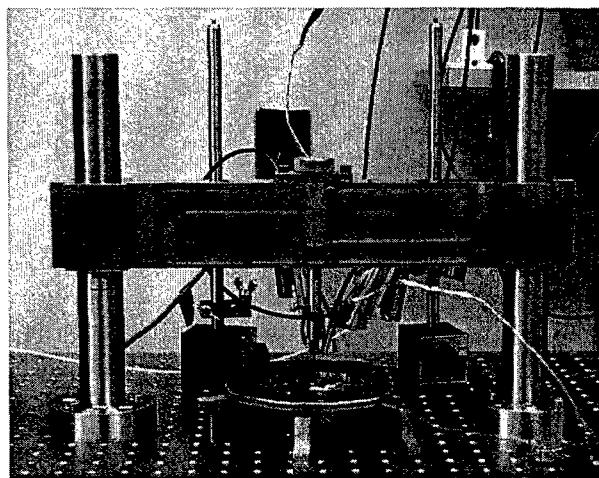


Figure 4. Piezo-electric device for direct measurement of middle ear stapes footplate.

Middle Ear Anatomy

A number of different hypotheses have been put forth over the years about how the cetacean middle ear might function. Many of these hypotheses seemed to us to lack



Figure 5. Ossicular chain of a bottlenose dolphin ear reconstructed from micro CT images. Malleus (yellow); incus (green); stapes (orange)

biophysical plausibility. We decided to take a fresh look at the middle ear anatomy in odontocetes with an eye towards creating a detailed model biomechanical model by employing microCT to scan ears from our two control species, harbor porpoise and bottlenose dolphin (Fig. 5)

The major attachment points for the malleus-incus complex are the processus gracilis and the minor process of the incus. These points define the most likely axis of rotation for the malleus-incus complex. Since the processus gracilis is fused with the tympanic bone, it appears that this structure acts as a torsional spring which may help to stiffen the middle ear. Although the shapes of the incus and malleus differ considerably from terrestrial mammals, this arrangement of the incus and malleus is very similar to that found in high-frequency terrestrial mammals.

The dolphin stapes is attached to the major process of the incus which acts as a lever arm. The tympanic ligament attaches to a longer lever arm on the malleus (Fig. 5). The tensor tympani muscle attaches to the same point, but from the opposite side, and is oriented so as to pull on the tympanic ligament when it contracts. This orientation of the tensor tympani with respect to the tympanic ligament is the same as that found in terrestrial mammals. The stapedial muscle is oriented at right angles to the motion of the stapes which is also the same orientation as that found in terrestrial mammals. Our anatomical studies provide further support for the hypothesis that the cetacean middle ear works in a fashion very similar to that of high-frequency terrestrial mammals and that the tympanic ligament plays a major role in producing middle ear motion in response to sound.

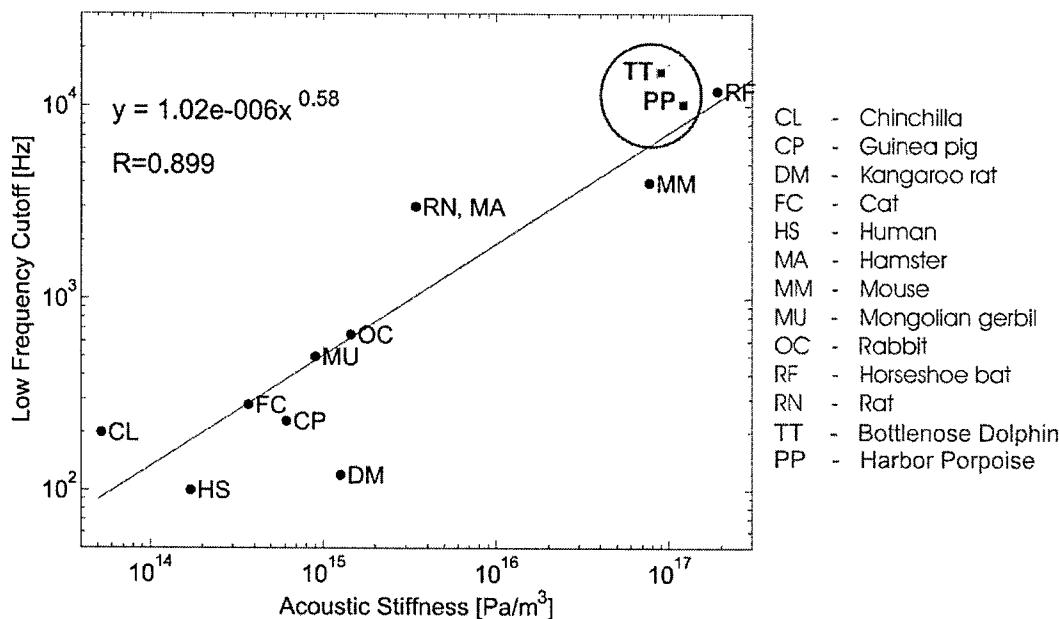


Figure 6. Low Frequency Limits of hearing vs Middle Ear Stiffness.

The fact that the odontocete middle ear appears to function in a manner similar to that found in terrestrial mammals means that generic biophysical models of middle ear function can be used to predict middle ear function in cetaceans. The curve shown in Figure 6 is especially important because it suggests that we can get an estimate of low-frequency hearing sensitivity through simple measurements of middle ear stiffness.

Basilar Membrane Mechanics

The range of hearing in mammals and especially the high-frequency limit is believed to be determined by the basilar membrane frequency-place map. In terrestrial mammals, the basilar membrane near the base of the cochlea is much stiffer than it is near the cochlear apex. As a result, the basal portion of the membrane responds best to high frequencies and the apical portion of the membrane responds best to low frequencies.

To measure basilar membrane stiffness in cetaceans, we used a force probe that is similar in concept to that used for the middle ear measurements but which is much more sensitive. The dolphin stiffness gradient is very similar to that for gerbil but exhibits a higher stiffness. If basilar membrane mechanics in the two species are similar, the higher stiffness for dolphin is to be expected since the high-frequency limit for the bottlenose dolphin is about 2.5 times that for gerbil.

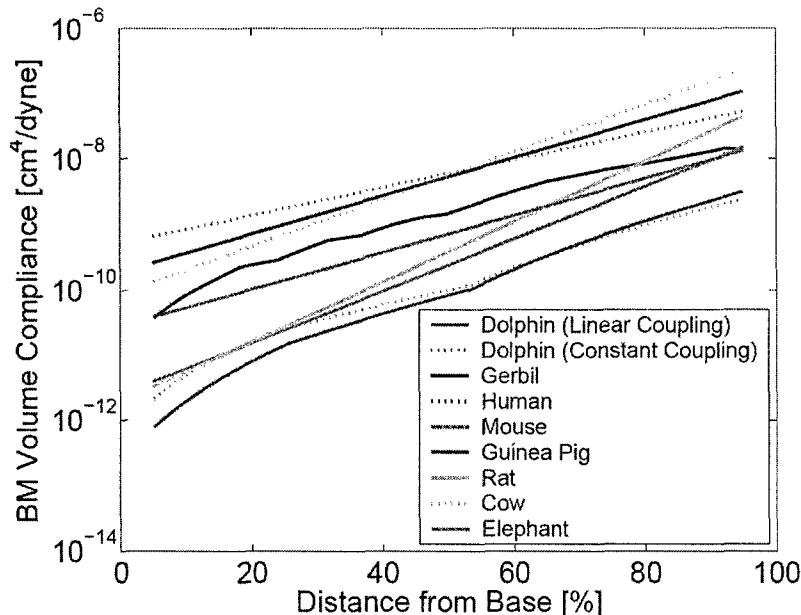


Figure 7. Bottlenose dolphin basilar membrane volume compliance compared to 7 terrestrial species. All data except dolphin and gerbil are from von Bekesy (1960).

Von Bekesy (1960) published data for basilar membrane volume compliance from a number of different species. In Figure 7 we have converted our gerbil and dolphin stiffness data into volume compliance and plotted our data along with the von Bekesy data. All of the species show similar compliance gradients and the dolphin curve exhibits the lowest compliance (highest stiffness) as would be expected for a high frequency ear.

Summary

Our anatomical and mechanical measurements in control species support the hypothesis that the cetacean middle ear and cochlea function in a manner very

similar to that of terrestrial mammals. This means that the computational models that we have developed to predict hearing function in terrestrial mammals can be extended directly to cetaceans. Our next step is to extend the middle ear and cochlear measurements to multiple specimens and species of special concern (e.g. beaked and baleen whales) and to use our computational models to predict audiograms for these species.

IMPACT/APPLICATIONS

National Security

Both research and U.S. Navy operations are hampered by intense public oversight and even injunction because of a lack of knowledge about the hearing and the mechanisms and specificity of acoustic impacts for many marine mammals. These concerns are particularly acute for effects of sonars on whales and dolphins. The development of robust, marine-explicit auditory models will allow us to estimate audiograms for multiple odontocete species from anatomical and mechanical measurements and to predict the excitation pattern within individual cochlea for a range of acoustic inputs, as well as model stresses and strains on key cochlear tissues from overstimulation.

In addition to the on-going work by NRL on this project and the ties to the ESME effort, both Dr. Ketten and Dr. Mountain presented briefings on the use of these models to predict cetacean hearing capabilities at NUWC-Newport, Groton, and the Dive Physiology Groups at NUWC and Panama City. This has led to discussions about how we might collaborate on joint projects. Technical points of contact are Dr. Tariq Manzur, Dr Wayne Gerth, and Dr. Edward Cudahy.

Economic Development

All three principal laboratories for this effort will develop web-accessible data bases and publicly accessible representative samples of this work. The databases are expected to be open architecture and structured for ease of export and cross-application access. The publicly accessible data will enable informed assessment of risks from manmade underwater sound such as sonars, ships machinery, and industrial activity.

Both Dr. Ketten and Dr. Mountain were invited panelists and discussants for the International Workshop on Sound and the Marine Environment sponsored by the International Oil and Gas Producers' Association, Halifax, Nova Scotia, August 30 – September 1, 2005 and have on-going discussions with representatives of this industry as well as shipping interests about the applicability of this research to their compliance requirements.

Quality of Life

At present, there are broad scientific and public concerns about potential impacts of human sound sources in the oceans. These models will provide new, explicit

information on the functional organization and acoustic response characteristics of whale ears and on neural and mechanical elements of whale hearing. Further, they will provide the first models of the mechanisms and potential magnitude of threshold shifts in multiple cetacean species.

Science Education and Communication

All three principal laboratories for this effort are developing web-accessible data bases and publicly accessible representative samples of this work. BU has already begun producing a web-site for review of available audiograms and as part of their on-going EarLab project and has the infrastructure to extend their site to incorporate the inner ear models. It is also expected that a simple, ESME-like model will be produced that can be run from the website that includes marine species for which there are reliable hearing data as well as sample sources with appropriate distance effects in their renditions, including biologic, commercial, exploratory, and military sources.

The WHOI laboratory is developing a website featuring CT images and reconstructions for representative marine mammal species and will incorporate the new beaked whale data in that site production. The proto-website is expected to be on-line early October, 2006.

NRL anticipates developing web-friendly renderings that allow visitors to explore the substructure of the heads at the gross level and will assist with the development and implementation of the ESME format model. All sites will incorporate links to all team laboratory websites.

The databases are expected to be open architecture and structured for ease of export and cross-application access

RELATED PROJECTS

Both the BU and WHOI laboratories have NIH supported and collaborative efforts related to cochlear modeling, primarily of land based species.

PUBLICATIONS

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